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INSTRUCTIONS TO AUTHORS

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        Number of illustrations (figures, enumerated maps and tables, in this order)
    (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
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    (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
    (f) *Summary*, if paper is lengthy
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    Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

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    Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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        'Smith (1969) describes . . .'
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        For books give title in italics, edition, volume number, place of publication, publisher.
        For journal article give title of article, title of journal in italics (abbreviated according to the *World list o, scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination (first and last pages of article).

        Examples (note capitalization and punctuation)

        BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
        FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* 88: 100–140.
        FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627–634.
        KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309–320.
        KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1–51.
        THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269–270.

EARLY PLIOCENE PROCELLARIIFORMES (AVES) FROM LANGEBAANWEG, SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

By

STORRS L. OLSON

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By

STORRS L. OLSON

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(With 7 figures and 5 tables)

ABSTRACT

Eight species of sea-birds of the order Procellariiformes are identified among the fossils collected from early Pliocene deposits at Langebaanweg, south-western Cape Province, South Africa. All four living families of Procellariiformes are represented, including an albatross (Diomedeidae), a new species of *Oceanites* ('*Pelagodroma*', Oceanitidae), five species of Procellariidae, including three species of *Pachyptila*, one of which is described as new, and a new species of diving petrel (Pelecanoididae). At least three of these species appear to have been breeding in the area, indicating that cold Temperate or Subantarctic oceanic conditions were present in the south-western Cape in the early Pliocene. The specimens of *Oceanites, Pachyptila*, and *Pelecanoides* provide the first Tertiary records for these genera. Most taxa are very similar to and perhaps ancestral to living species, with the principal exception of a giant form of *Pachyptila* that represents a previously unknown lineage.

CONTENTS

INTRODUCTION

Among the abundant fossils of terrestrial and aquatic birds from the early Pliocene deposits at Langebaanweg (P. Rich 1980) are remains of at least eight species representing each of the four families of the strictly marine order Procellariiformes (albatrosses, storm-petrels, shearwaters, and diving petrels). The only other site in South Africa from which Tertiary procellariiform fossils have been recovered is at Duinefontein, also in the south-western Cape and of approximately equivalent age (Olson in press *a*). The palaeoceanographic significance of the marine birds from these early Pliocene faunas is dealt with in a more general overview (Olson 1983), the scope of the present paper being mainly systematic.

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The geology and chronology of the Langebaanweg sequence have been detailed by Hendey (1981*a*, 1981*b*, 1982). These deposits formed during an early Pliocene period of marine transgression, under a variety of estuarine and fluviatile conditions that resulted in the accumulation of remains of both marine and terrestrial organisms. The Langebaanweg sequence comprises two lithostratigraphic units, the Quartzose Sand Member (QSM) and the Pelletal Phosphorite Member (PPM). The PPM consists of channel deposits in two different beds, 3aS and 3aN, the latter of which truncates the former and is thus younger, at least where palaeontological excavations were undertaken. Both the QSM and PPM are time-transgressive so that whereas parts of the QSM are older than parts of the PPM, this relationship does not hold throughout the entire sequence (see Hendey 1981*b*: 32, fig. 8). There is sufficient evolutionary time represented between the older and younger portions of the sequence for morphological changes to have taken place within some species of mammals, e.g. the seal *Homiphoca capensis* (De Muizon & Hendey 1980).

Most of the individuals of Procellariiformes come from the QSM deposits (Table 5), indicating that this unit probably had a somewhat stronger marine influence than the PPM deposits. The composition of species and individuals of marine birds and the preservation of the bones themselves contrast with more typical marine deposits such as at Duinefontein, and indicate that at least the more abundant species were probably breeding in the vicinity, where they could have taken advantage of nearby islands that were created by the higher sea levels of the early Pliocene (Olson 1983).

Fossil specimens described here are in the collections of the division of Cenozoic Palaeontology of the South African Museum; all fossil specimen numbers are prefixed by the acronym SAM–PQ, which has been omitted here for the sake of brevity.

SYSTEMATICS

Order Procellariiformes
Family **Diomedeidae**
Genus *Diomedea* Linnaeus, 1758
Diomedea sp.

Material

Proximal end of left tarsometatarsus L12005, from the Quartzose Sand Member of the Varswater Formation at Langebaanweg.

Discussion

This single bone is the only evidence to date of albatrosses from the Tertiary of South Africa. The specimen is porous proximally and hence is from a juvenile individual and may indicate breeding in the vicinity. The proximal width is 17,3 mm, the specimen being from a species approximately the size of the living *Diomedea melanophris*.

Although albatrosses today are predominantly birds of southern oceans, there are but two other Tertiary records from the Southern Hemisphere—a fragmentary rostrum from the late Miocene of Victoria, Australia, described as *Diomedea thyridata* (Wilkinson 1969), and a single toe bone of a larger species from the early late Miocene near the Valdez Peninsula, Argentina (Olson 1984). This contrasts with the much better representation of albatrosses in the Northern Hemisphere where fossils are known from the late Oligocene into the Quaternary (Olson in press *b*).

Family **Oceanitidae**

Subfamily Oceanitinae

Both on osteological and myological grounds, the storm-petrels fall into two very distinct groups that are best ranked as subfamilies (see Klemm 1969). The more specialized of these, to which all the fossils from Langebaanweg clearly belong, is the Oceanitinae, characterized by very short, stout humeri, ulnae, and femora, and greatly elongated tibiotarsi and tarsometatarsi. Five genera are customarily admitted among the species in the Oceanitinae (e.g. Jouanin & Mougin 1979), but I am unable to discern any osteological basis for considering either *Pelagodroma* Reichenbach, 1853, or *Garrodia* Forbes, 1881, to be distinct from *Oceanites* Keyserling & Blasius, 1840. *Pelagodroma marina* and *Garrodia nereis* resemble each other and differ from *Oceanites oceanicus* and *O. gracilis* in having the rostrum longer and more slender and the ridge of bone between impressions of the supraorbital glands narrower, but neither of these characters can be regarded as being of generic importance. Hence the first two are included in *Oceanites* as *O. marinus* (Latham) and *O. nereis* (Gould), respectively.

Within the Oceanitinae, there is an evolutionary trend towards greater size and increasing specialization of the tarsometatarsus and toes for locomotion across the surface of the water. In *Oceanites* this can be described as paddling, whereas *Fregetta* and *Nesofregetta* use the feet to bound rapidly across the surface, often against strong head winds (D. G. Ainley, Point Reyes Bird Observatory, pers. comm.). The trend for morphological specialization for such locomotion reaches its extreme in *Nesofregetta fuliginosa*, which is the largest species in the family and in which the distal end of the tarsometatarsus is expanded and the toes are greatly flattened, being fused by the skin of the web into a nearly inflexible paddle. The two species of *Fregetta* are more or less intermediate in these respects between *Oceanites* (*sensu lato*) and *Nesofregetta*. Within *Oceanites, O.* ('*Pelagodroma*') *marinus* shows perhaps the greatest tendency towards the specializations of *Fregetta* and *Nesofregetta*.

Genus *Oceanites* Keyserling & Blasius, 1840 (*sensu lato*)

All the storm-petrel bones from Langebaanweg are referable to a single species of Oceanitinae that differs from *Fregetta* in having the tibiotarsus and tarsometatarsus proportionately longer and much more slender. It differs from

Nesofregetta in lacking the distinctly flattened and expanded distal end of the tarso-metatarsus and thus agrees with *Oceanites* in the broad sense as defined above.

Oceanites zaloscarthmus sp. nov.

Figs 1–2

Material

Holotype: L25214, complete right humerus (Fig. 1A), from the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

Paratypes: In addition to the holotype, 175 other specimens are referred to this species. These consist of 2 right and 2 left coracoids; 6 complete, 7 proximal, and 11 distal right humeri; 6 complete, 5 proximal, and 17 distal left humeri; 6 complete and 2 distal right ulnae; 4 complete, 3 proximal, and 4 distal left ulnae; 2 proximal left carpometacarpi; 4 right and 6 left femora; 14 distal right, 3 proximal left, and 16 distal left tibiotarsi; 2 complete, 17 proximal, and 10 distal right tarsometatarsi; 1 complete, 13 proximal, and 13 distal left tarsometatarsi. A list of specimen numbers with exact provenance within the Langebaanweg quarry is kept at the South African Museum and is also available from the author. The two carpometacarpi were found in unsorted material and some of the femora were in amongst the Passeriformes, so additional specimens of the species will doubtless be found in the material that has already been collected.

Measurements of holotype

Total length 24,80 mm; length from distal end of pectoral crest to distal extent of dorsal condyle 17,70 mm; width of shaft at midpoint 2,20 mm; distal width 4,80 mm. (Measurements to nearest 0,05 mm.)

Measurements of paratypes

See Table 1.

Diagnosis

Much larger and more robust than *Oceanites oceanicus, O. gracilis,* or *O. ('Garrodia') nereis.* Very similar in size and morphology to *O. ('Pelago-droma') marinus* but (1) brachial fossa of humerus much shallower and less extensive; (2) olecranon better developed (nearly absent in *O. marinus*); (3) carpal tubercle of ulna more pointed, less expanded and less triangular; (4) distal end of ulna not rotated ventrally; (5) shafts of hindlimb elements more robust; (6) femur less curved in lateral and medial views; (7) wings of inner and outer trochleae of tarsometatarsus less prominent and not as expanded to the sides.

Distribution

Early Pliocene Varswater Formation (QSM, PPM 3aN, PPM 3aS) at Langebaanweg, south-western Cape Province, South Africa.

TABLE 1

Skeletal measurements (to nearest 0,05 mm) of fossil and
living species of *Oceanites* (*'Pelagodroma'*).

| | O. zaloscarthmus sp. nov. | | | O. marinus (n = 3*) | |
	n	range	mean	range	mean
CORACOID					
Length from head to midpoint					
of sternal end	3	13,35–13,60	13,50	13,80–14,00	13,90
Shaft width at midpoint	4	1,60–1,95	1,75	1,45–1,70	1,55
HUMERUS					
Total length	10	24,80–26,50	25,75	24,30–25,15	25,00
Length from distal end of pectoral					
crest to dorsal condyle	21	17,55–19,65	18,75	17,50–18,55	18,10
Shaft width at midpoint	30	1,90–2,50	2,25	1,95–2,10	2,00
Distal width	35	4,25–5,25	4,75	4,60–4,75	4,65
ULNA					
Total length	5	22,60–23,50	23,10	22,10–22,95	22,60
Length from distal lip of ventral					
cotyla to distal end	9	20,95–21,95	21,50	20,45–21,45	21,10
Shaft width at midpoint	14	1,75–2,20	2,00	1,80–1,90	1,85
Distal width	18	3,20–3,85	3,40	3,30–3,55	3,40
CARPOMETACARPUS					
Proximal depth	2	4,85–4,90	4,90	4,90–5,00	4,95
FEMUR					
Total length	8	16,20–17,50	16,65	17,00–17,25	17,15
Proximal width	7	4,10–4,40	4,30	4,00	4,00
Shaft width at midpoint	10	1,70–1,90	1,80	1,65	1,65
Distal width	2	3,75–3,95	3,85	3,70–4,20	3,90
TIBIOTARSUS					
Distance from proximal articular					
surface to distal end of					
fibular crest	3	11,55–13,80	12,75	12,65–14,05	13,25
Distal width	24	3,55–3,85	3,70	3,50–3,65	3,60
TARSOMETATARSUS					
Total length	3	40,40–41,80	40,90	39,05–40,45	39,95
Proximal width	29	3,90–4,55	4,35	4,20–4,35	4,30
Shaft width at midpoint	14	1,70–2,10	1,85	1,60–1,67	1,65
Distal width	24	4,25–4,80	4,45	4,45–4,50	4,50

* Two skeletons from Peru and one from South Africa.

Etymology

Greek *zale*, surging sea, and *skarthmos*, skipping; essentially a rephrasing of the word *pelagodroma*.

Remarks

Except for the distinguishing features of the humerus and ulna, the differences between *Oceanites zaloscarthmus* and *O. marinus* are very minor and
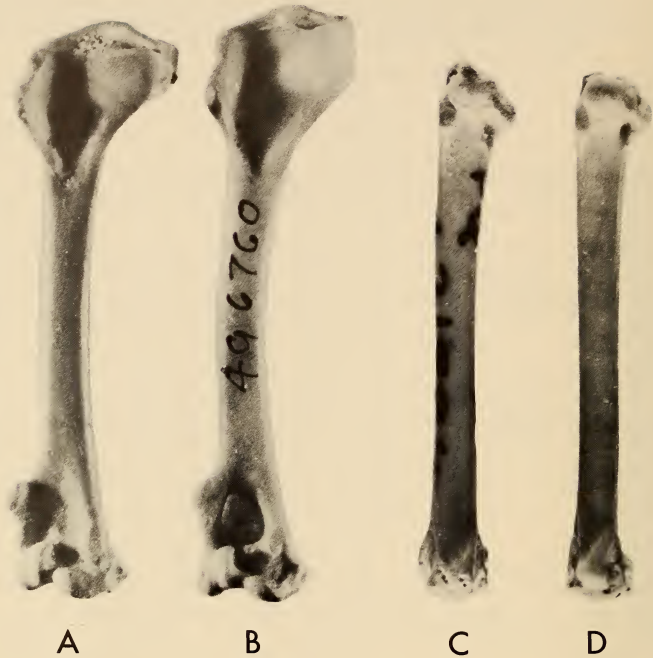
Fig. 1. Wing elements of *Oceanites* (*'Pelagodroma'*).   A. *O. zaloscarthmus* sp. nov., holotype, L25214, right humerus, cranial aspect.   B. *O. marinus*, USNM 496760, right humerus, cranial aspect.   C. *O. zaloscarthmus* sp. nov., L21994, left ulna, cranial aspect. D. *O. marinus*, USNM 496760, left ulna, cranial aspect.   All figures × 3.

it is likely that the Langebaanweg species is ancestral to the living form. A more specialized condition in the latter is the curious rotation of the distal end of the ulna ventrally (Fig. 1C, D) with respect to the 'standard anatomical position' (Baumel 1979: 5). This is best appreciated when the ulnae are viewed resting on the caudal (trailing) surface (i.e. with the secondary papillae downward—see Fig. 1C, D). The deepening of the brachial fossa of the humerus and the reduction of the olecranon in *O. marinus* may possibly be correlated with the ventral rotation of the distal end of the ulna.

The fossils from Langebaanweg constitute only the fourth reported Tertiary occurrence of the family Oceanitidae. The others consist of two specimens from the late Miocene of California referred to the genus *Oceanodroma* (see Howard
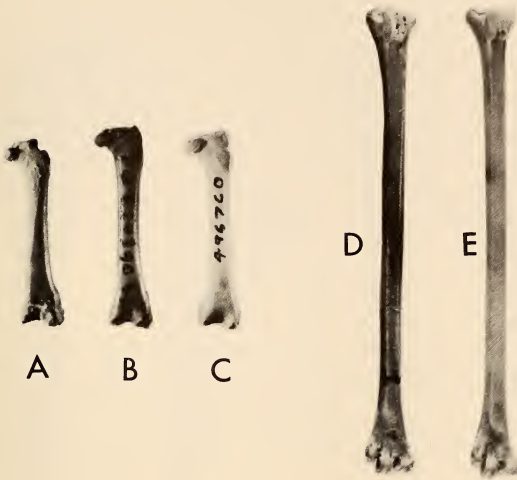
Fig. 2. Hindlimb elements of *Oceanites ('Pelagodroma')*.
A–B. *O. zaloscarthmus* sp. nov., L24405, L24390U, left femora in cranial aspect showing variation in size and robustness. C. *O. marinus*, USNM 496760, left femur, cranial aspect. D. *O. zaloscarthmus* sp. nov., L24386Q, right tarsometatarsus, plantar aspect. E. *O. marinus*, USNM 496760, right tarsometatarsus, plantar aspect. All figures × 2.

1978), and the shaft of a humerus the size and shape of that of *Oceanites oceanicus* from Duinefontein (Olson in press *a*). Despite the relative abundance of *Oceanites zaloscarthmus* at Langebaanweg, the species is entirely absent at Duinefontein. This may reflect differences in the depositional environment at these two sites. That so many bones of *O. zaloscarthmus* were concentrated at Langebaanweg is an almost certain indication that the species was breeding close by, probably on the islands lying immediately offshore from the Langebaanweg site (Hendey 1981*b*, 1982; Olson 1983, in press *a*). The probable presence of a breeding colony is also indicated by incompletely ossified bones of young, though possibly volant, individuals among the fossil sample.

The living species *Oceanites marinus* is rather widely distributed, nesting on islands in waters that lie in warm Subantarctic and especially in cool Subtropical waters. Although the species disperses widely in the non-breeding season, it has not as yet been recorded from South African waters (Clancey 1980; Harrison 1983). There are breeding populations on islands around western and southern Australia, in the New Zealand region, and in the Atlantic in the Salvages, Cape Verdes, and Tristan da Cunha (Jouanin & Mougin 1979). The species was once

abundant at St. Helena, probably until after the arrival of man in the sixteenth century (Olson 1975), and bones are also known from Madeira and Porto Santo (Harald Pieper, Zoologisches Museum, Kiel, pers. comm.). The species disappeared in relatively recent times from Amsterdam Island in the Indian Ocean (Jouanin & Paulian 1960), probably as the result of introduced predators (Murphy & Irving 1951). The absence of *O. marinus* in the Benguela Current off South Africa is the more curious considering that the species is quite abundant in the Peru Current off South America, which would seem to present similar conditions. This might be due in part to the extirpation of the population on St. Helena, although one might expect birds from Tristan da Cunha off South Africa as well.

Family **Procellariidae**

Genus *Pachyptila* Illiger, 1811

The prions (*Pachyptila*) are unique among the Procellariidae in having the bill greatly expanded and equipped with lamellae for filtering small prey items. The tongue and hyoid apparatus are correspondingly enlarged and housed in a distensible gular sac. With the exception of the very tip of a rostrum, however, cranial elements of *Pachyptila* have not yet been identified from Langebaanweg and fossils from there are assigned to this genus on the basis of characters of the humerus, which in *Pachyptila* has a short, blunt ectepicondylar spur (processus supracondylaris dorsalis) in combination with a very deep brachial fossa, terete shaft, and lack of expansion of the ventral epicondylar area. The humerus of *Pachyptila* is most similar to that of *Halobaena*, but in that genus the ventral epicondylar area is slightly expanded and the ectepicondylar spur is deeper proximo-distally.

Pachyptila salax sp. nov.

Figs 3–5, 6A

Material

Holotype: L25187, complete left humerus (Figs 3A, 6A) from the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

Paratypes: In addition to the holotype, 202 other specimens are referred to this species. These consist of 3 complete, 1 scapular, and 1 sternal ends of right coracoids; 8 complete, 4 scapular, and 1 sternal ends of left coracoids; 1 nearly complete, 14 proximal, and 16 distal right humeri; 1 nearly complete, 7 proximal, and 13 distal left humeri; 4 proximal and 4 distal right ulnae; 2 complete, 2 proximal, and 4 distal left ulnae; 3 proximal and 1 distal right carpometacarpi; 2 complete and 2 proximal left carpometacarpi; 1 complete and 3 proximal right femora; 3 complete, 3 proximal, and 1 distal left femora; 11 right and 5 left distal ends of tibiotarsi; 7 complete, 13 proximal, and 7 distal right tarsometatarsi; 5 complete, 9 proximal, and 8 distal left tarsometatarsi. With less certainty,

Fig. 3. Wing elements of *Pachyptila*.   A. *P. salax* sp. nov., holotype, L25187, left humerus, caudal aspect.   B. *P. vittata*, SAM–ZO56746, left humerus, caudal aspect.   C. *P. salax* sp. nov., L22224, left ulna, dorsal aspect.   D. *P. vittata*, SAM–ZO56746, left ulna, dorsal aspect.   All figures × 2.

4 scapulae, 2 fragments of sterna, the distal end of a radius, and 25 pedal phalanges are assigned to this species on the basis of size. A list of specimen numbers with exact provenance within the Langebaanweg quarry is kept at the South African Museum and is also available from the author.

Measurements of holotype

Total length 73,1 mm; length from head to proximal lip of brachial fossa 62,5 mm; length from distal end of pectoral crest to distal end of dorsal condyle 54,7 mm; proximal width through dorsal and ventral tubercles 12,7 mm; width and depth of shaft at midpoint 4,3 and 3,7 mm; distal width 9,3 mm.

Measurements of paratypes

See Tables 2 and 3.

Diagnosis

Much larger than any known species of *Pachyptila* (Table 2). Apart from size, there are few postcranial characters that will distinguish between the species of *Pachyptila*, although in *P. salax* the carpal tubercle of the ulna appears less pointed and slightly more proximally situated, the alular metacarpal and extensor process are more perpendicular to the shaft rather than slanting proximally, and the shaft of the tarsometatarsus appears to be relatively stouter.

Distribution

Early Pliocene Varswater Formation (QSM, PPM 3aN, PPM 3aS, and Duynefontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

Etymology

Greek *salax*, a sieve, in allusion to the filtering apparatus characteristic of the living members of this genus. The name is a masculine noun in apposition and there is no implied allusion to the pejorative Latin adjective of the same orthography.

Remarks

Pachyptila salax is so much larger than any of the living taxa in the genus (Table 2), regardless of their status, that there can be no question of its specific distinctness. It was a giant among prions and adds an entirely new dimension to our concept of radiation within *Pachyptila*. Although prions the size of *P. salax* may have been endemic to South Africa, it seems likely that birds of this size class would have been more widely distributed in the past and have become extinct everywhere since the early Pliocene.

It is unfortunate that there is not more of the bill known for *P. salax*. The tip of a rostrum that is tentatively referred to this species (Fig. 5A, C) is not sufficient even to suggest how much the rest of the bill may have been expanded. Compared

TABLE 2

Measurements (mm) of living and fossil taxa of *Pachyptila*.

Measurement No.	*turtur* n = 3		*crassirostris* n = 1	*belcheri* n = 8		*desolata* n = 11		sp. C n = 3		*salvini* n = 8		*vittata* n = 5		sp. B n = 1	*sulax* sp. nov.		
	range	mean	mean	range	mean	range	mean	range	mean	range	mean	range	mean	mean	n	range	mean
1	52,2–54,8	53,6	56,9	54,5–57,0	55,9	54,8–60,0	57,5	—	—	56,1–59,0	57,7	58,4–61,1	59,6	—	1	—	73,1
2	2,7–3,0	2,9	3,2	3,3–3,7	3,4	3,1–3,7	3,4	—	—	3,4–3,9	3,6	3,6–3,8	3,7	—	8	4,1–4,8	4,4
3	6,2–6,9	6,6	7,5	7,3–7,9	7,5	7,1–7,8	7,5	6,3–7,4	6,8	7,5–8,1	7,8	7,9–8,3	8,1	7,8	14	8,9–10,1	9,5
4	49,4–54,3	51,6	55,0	51,6–55,2	53,3	52,4–59,2	55,9	—	—	54,0–57,7	56,2	58,3–61,9	60,2	—	2	72,7–75,0	73,9
5	26,8–29,2	28,2	30,2	28,8–30,1	29,5*	28,6–31,3	30,1	—	—	29,2–31,7	30,3	31,5–33,8	32,7	—	2	37,4–39,5	38,5
6	22,9–24,2	23,9	25,9	22,8–24,5	23,6*	23,5–24,8	24,3*	—	—	23,8–26,2	24,8	25,3–26,0	25,7*	—	3	30,6–32,9	31,8
7	32,0–33,2	32,5	34,7	31,2–34,3	32,8	31,8–34,1	33,0	—	—	30,9–34,8	32,8	33,3–35,2	34,2	—	12	36,5–39,2	37,6

* n = one less than listed above.

Measurements are: 1. length of humerus; 2. shaft width of humerus at midpoint; 3. distal width of humerus; 4. length of ulna; 5. length of carpometacarpus; 6. length of femur; 7. length of tarsometatarsus.

TABLE 3

Additional measurements (mm) of *Pachyptila salax* sp. nov.

	n	range	mean
CORACOID			
Length from head to medial angle	9	22,4–24,2	23,3
HUMERUS			
Proximal width through dorsal and			
ventral tubercles	6	12,5–13,3	12,9
Length from distal end of pectoral crest			
to dorsal condyle	4	52,2–54,7	53,7
Length from head to proximal lip of			
brachial fossa	3	62,5–65,3	64,2
ULNA			
Proximal width	7	5,7–6,5	6,2
Distal width	6	5,5–5,9	5,7
CARPOMETACARPUS			
Proximal depth	3	8,9–9,2	9,1
Proximal width	5	6,9–7,3	7,1
Distal width	2	6,5–6,5	6,5
TIBIOTARSUS			
Distal width	12	5,1–5,5	5,4
TARSOMETATARSUS			
Proximal width	30	5,8–6,8	6,4
Shaft width at midpoint	19	2,4–3,1	2,6
Distal width	22	5,6–6,7	6,2

with *P. vittata*, the rostral tip of *P. salax* is markedly broader and considerably less decurved.

On size alone there are at least three species of *Pachyptila* in the Langebaanweg fauna and also at Duinefontein (Olson in press *a*). *Pachyptila salax* is larger than any other species in the genus, *Pachyptila* species B (see p. 138) is the size of the two largest living taxa, *P. vittata* and *P. salvini*, and *Pachyptila* species C (see p. 138) falls within the size ranges of the four smaller living taxa (Table 2). It is possible that more than one species could be included under *Pachyptila* species C. The available specimens of *Pachyptila* species B and C, all postcranial, are insufficient to determine anything more than that at least two species are represented. Although these fossils cannot be distinguished from living taxa, they cannot be assigned to a particular living taxon nor can one

(facing page)

Fig. 4.   Skeletal elements of *Pachyptila*.   A. *P. salax* sp. nov., L28203U, left carpometacarpus, ventral aspect.   B. *P. vittata*, SAM–ZO56746, left carpometacarpus, ventral aspect.   C. *P. salax* sp. nov., L28174C, right coracoid, ventral aspect.   D. *P. vittata*, SAM–ZO56746, right coracoid, ventral aspect.   E. *P. salax* sp. nov., L25531, right femur, cranial aspect.   F. *P. vittata*, SAM–ZO56746, right femur, cranial aspect.   G. *P. salax* sp. nov., L20691M4, left tarsometatarsus, cranial aspect.   H. *P. salax* sp. nov., L24397, right tarsometatarsus, cranial aspect (note variation in robustness of shaft).   I. *P. vittata*, SAM–ZO56746, right tarsometatarsus, cranial aspect.   All figures × 2.

A   B   C   D
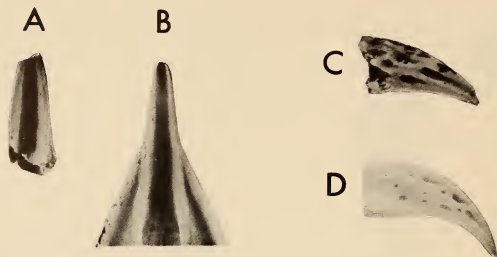
E   F   G   H   I

Fig. 5. Rostral tips (premaxillae) of *Pachyptila*.   A. *P. salax*
sp. nov., L28857, ventral aspect.   C. Same, lateral aspect.
B. *P. vittata*, SAM–ZO56746, ventral aspect.   D. Same, lateral
aspect.   All figures × 2.

assume that the fossils actually were conspecific with any taxon now in existence.

The South African occurrences provide the first fossil record to date for the genus *Pachyptila*. The concentration of bones of *P. salax* at Langebaanweg and the presence of incompletely ossified bones, probably from pre-fledging individuals, show that at least *P. salax*, if not the other species of *Pachyptila*, was breeding in the vicinity of Langebaanweg. This indicates that Subantarctic or at least cool Subtropical marine conditions probably existed nearby. Today, most breeding colonies of *Pachyptila* are on islands in Antarctic or Subantarctic waters. The only colonies north of the Subtropial Convergence are at Tristan da Cunha, St. Paul and Amsterdam islands, and in the northern part of New Zealand, all of which lie quite near the Subtropical Convergence.

The systematics of the modern species of *Pachyptila* are quite complex and a consensus on the number of species that should be recognized has not been reached. The divergence in views is exemplified by Harper (1980), who continues to recognize the six species that have commonly been accepted, and Cox (1980), who advocates reducing the number to three (though his argument leads to only two species). Consideration of the osteology of *Pachyptila* makes it doubtful that the number of species can be as few as three. Were Cox correct, some of the species of *Pachyptila* would exhibit a degree of morphological plasticity with few parallels among sea-birds.

Fleming (1941) attributed much of the speciation process in *Pachyptila* to the effects of Quaternary climatic events. Whereas it is likely that some of the differentiation between populations that has caused problems in assessing relationships among living taxa may have arisen as late as the Quaternary, we have seen that considerable divergence and radiation had already taken place in *Pachyptila* by the early Pliocene. It seems probable, therefore, that the principal species lineages in *Pachyptila* arose prior to the Quaternary.

Fig. 6.   Left humeri (except C, distal end of right humerus) of *Pachyptila* in cranial aspect.
A. *P. salax* sp. nov., holotype L25187.   B. *P. vittata,* SAM–ZO56746.   C. *Pachyptila*
species B, L25577.   D. *Pachyptila* species C, L24386D, I.   E. *P. desolata*, SAM–ZO56324.
All figures × 2.

Pachyptila species B

Fig. 6C

Material

Distal end of right humerus, L25577DF; proximal end of right humerus, L42830D.

Distribution

Early Pliocene Varswater Formation (QSM, PPM 3aS, and Duynefontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

Remarks

This species is the size of *Pachyptila vittata* or *P. salvini*, the two largest living members of the genus, and cannot be distinguished from either on the basis of available material. See remarks under *P. salax*.

Pachyptila species C

Fig. 6D

Material

Complete left humerus, L24386D, I; distal ends of left humeri, L25776BO, L25575B; distal end of right humerus, L25579G2.

Distribution

Early Pliocene Varswater Formation (QSM and Duynefontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

Remarks

This species is the size of the smaller living taxa of *Pachyptila* but the material is not otherwise diagnostic—see remarks under *P. salax*. Nine pieces of ulnae, two coracoids, and the distal end of a tibiotarsus are from procellariids too small for *Pachyptila salax*. These most likely belong to one or the other of the smaller species of *Pachyptila*.

Genus *Puffinus* Brisson, 1760

Subgenus *Puffinus* Brisson, 1760

Puffinus sp.

Material

Distal end of right humerus, L25577CF; proximal end of left humerus, L56198; right coracoid, L25481.

Distribution

Early Pliocene Varswater Formation (QSM, PPM 3aN, and Duynefontyn Members) at Langebaanweg and Duinefontein, south-western Cape Province, South Africa.

Remarks

This is '*Puffinus* species B' of the Duinefontein fauna. It is similar in morphology to the living short-tailed shearwater, *Puffinus tenuirostris*, and was about the same size, although perhaps slightly smaller. It is illustrated and is discussed more fully elsewhere (Olson in press *a*).

Procellariidae gen. et sp. indet.

Material

Left coracoid, L28440J.

Distribution

Early Pliocene, Quartzose Sand Member of the Varswater Formation at Langebaanweg, south-western Cape Province, South Africa.

Remarks

This specimen is from a procellariid larger than *Pachyptila salax* and smaller than the preceding species; thus it represents an additional taxon for Langebaanweg. The bone differs qualitatively from any of the species of *Puffinus* and is compatible in size with the enigmatic species of fulmarine from Duinefontein (Olson in press *a*).

Family **Pelecanoididae**

Genus *Pelecanoides* Lacépède, 1799

The flattened alcid-like humerus and the distinctive lateral reflection of the head of the coracoid make the three bones discussed below unmistakably referable to the monogeneric family of diving petrels. All three fossils appear to belong to a single species that differs only in minor details from living species of *Pelecanoides*.

Pelecanoides cymatotrypetes sp. nov.

Fig. 7

Material

Holotype: Complete left humerus, L14564 (Fig. 7A) from the Quartzose Sand Member of the Varswater Formation at Langebaanweg, Cape Province, South Africa.

Paratypes: Proximal end of left humerus lacking internal tuberosity, L28469T; left coracoid lacking parts of procoracoid and sternocoracoidal processes, L28855.
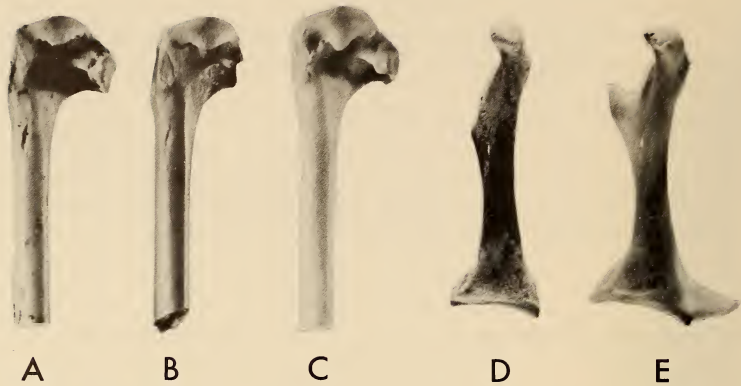
Fig. 7. Proximal portions of left humeri in caudal aspect (A–C) and left coracoids in ventral aspect (D, E) of *Pelecanoides*.   A. *P. cymatotrypetes* sp. nov., holotype, L14564. B. *P. cymatotrypetes* sp. nov., L28469T.   C. *P. urinatrix exsul*, USNM 553240. D. *P. cymatotrypetes* sp. nov., L28855.   E. *P. urinatrix exsul*, USNM 553242.

Measurements of holotype

Total length 43,2 mm; proximal width 9,2 mm; shaft width and depth at midpoint 3,4 and 2,1 mm; distal width 7,1 mm.

Measurements of paratypes

See Table 4 for measurements of coracoid.

Diagnosis

Differs from living species in lacking the distally projecting protuberance on the caudal surface of the head of the humerus; ventral tubercle in ventral view shorter and deeper. Coracoid with head projecting more ventrally and less medially than in living species.

Distribution

Early Pliocene, Quartzose Sand Member of the Varswater Formation at Langebaanweg, south-western Cape Province, South Africa.

Etymology

Greek *kyma*, wave, and *trypetes*, borer, from the habit of the living species of flying straight through the crests of waves. The name is a masculine noun in apposition.

Species	n	Humerus length	Coracoid length from head to midpoint of sternal facet
P. cymatotrypetes sp. nov.	1	43,2	24,6
P. urinatrix exsul	2	43,0; 44,1	23,2; 24,4
P. urinatrix chathamensis	1	40,6	21,8
P. urinatrix subsp. (Argentina)	1	42,1	22,9
P. magellani	2	43,3; 44,8	23,4; 25,1
P. georgicus	1	39,3	21,4

Remarks

This species is very similar to living forms except for the less extensive ossification of the head of the humerus, in which respect it is probably primitive. In size it is similar to *Pelecanoides urinatrix exsul* or *P. magellani*, but the bones are stouter than in the latter and the resemblances of the fossil are greatest to *P. u. exsul*.

The three bones of *P. cymatotrypetes* provide the only Tertiary record of the Pelecanoididae. A supposed Tertiary occurrence of *Pelecanoides* in New Zealand was subsequently shown to be Quaternary in age (T. Rich *et al.* 1979). Modern diving petrels are confined to cold Temperate or Subantarctic waters. None has been recorded from South Africa (Clancey 1980) and the nearest breeding colony is at Tristan da Cunha. Although considered to be 'sedentary' (Jouanin & Mougin 1979), high densities of diving petrels may occur some 1 300 to 1 600 km from the nearest land (D. G. Ainley, pers. comm.). They are nevertheless not as vagile as other members of the order.

DISCUSSION

Despite the fact that at present the order Procellariiformes is far more diverse in the Southern Hemisphere, its fossil record has hitherto been largely confined to the Northern Hemisphere, where the taxa represented consist mainly of albatrosses and a diversity of shearwaters of the genus *Puffinus* (Olson in press *b*). The early Pliocene deposits at Langebaanweg and at Duinefontein (Olson in press *a*) thus provide our first important insights into the procellariiform fauna of the southern oceans in the late Tertiary, as well as the first Tertiary records for the genera *Oceanites, Pachyptila*, and *Pelecanoides*.

The fossils available from deposits in the Northern Hemisphere seem to indicate that evolution within the Procellariiformes proceeded rather slowly from the Miocene onward, with species' lineages persisting for long periods with relatively little morphological change. Being extremely vagile, procellariiforms